DIEL CHANGES IN ICHTHYOFAUNAL ABUNDANCE AND COMPOSITION IN MIXED SPECIES SCHOOLS IN A CARIBBEAN REEF

MICHALE J. GLENNON AND JOANNA M. HUBBARD

Abstract. We examined diel changes in abundance, composition, and foraging ranges of mixed species schools of fish. Several studies have noted that the foraging rates of fish increase or experience a peak in the afternoon , which may result from increased quality of the food resource. We hypothesized that this diel pattern would result in observed changes in patterns of abundance, composition, age structure, and foraging area utilized in the morning versus the afternoon. We found more fish per school, more adults per school, greater species diversity, and less foraging distance traveled in the afternoon. Thus, changes in food quality throughout the day may influence behavior of fish and their use of schools as a mechanism of maximizing foraging efficiency.

INTRODUCTION

Mixed species schools of fish are common in the forereef area of Discovery Bay, Jamaica. We observed apparent differences in number of schools, number of fish per school, and age and species composition of schools during the morning and afternoon.

Itzkowitz (1976) found that peripheral species joined core species groups only for brief periods, indicating a high amount of variability of school composition between times.

Bruggeman et al. (1994) suggests that later in the day, ash content of macroalgal turf decreases, causing an increase in content of digestible material (mostly soluble carbohydrates). This is supported by findings that there is a feeding peak for herbivores starting around noon and ending at about 8 pm (Hay et al. 1988). It has been proposed that adults school primarily for feeding benefits while juveniles utilize schools for antipredator benefits as well as for feeding (Fields et al. 1993). These data indicate that the afternoon is the best time for herbivores to forage on the highest quality resource, and that if adults do school mainly to feed, they should be found in schools during the afternoon. Ruel et al. (1994) showed that fish in schools have higher feeding rates than solitary individuals. We would expect therefore, that fish should school most often when food is at the highest quality to achieve optimal foraging.

From these findings we hypothesized: 1) there are more mixed species schools in the afternoon than in the morning; 2) there are a greater number of individuals per school in the afternoon than in the morning; 3) there are more mature fish per school in the afternoon than in the morning; and 4) species composition of schools will be different between the morning and the afternoon.

In schools of more than two fish there is no leader and each fish adjusts its speed and direction to correspond with those of the surrounding fish (Partridge 1982), making it increasingly difficult to initiate movement in schools of increasing size. Due to this fact and the increase in forage quality in the afternoon, we further hypothesized that: 1) schools travel less distance in a given time during the afternoon than they do during the same amount of time in the morning and 2) schools will cover less area in a given time in the afternoon than they do during the same amount of time during the morning.

Mixed species schools contain invertibrate-eating fish as well as herbivorous ones. Losey (1978) suggests that, in schools, feeding on invertebrates is facilitated by grazing activities of the herbivorous fish. Therefore, we assumed that as the number of herbivorous fish in a school increases, more invertebrate-eating fish will become associated with schools. Thus, numbers of invertebrate-feeding and herbivorous fish should fluctuate together.

METHODS

Our study was conducted on 3-8 March 1995 at Discovery Bay Marine Laboratory, Jamaica. All data collection was done using SCUBA at the long term study site (LTS) at depths of 30 to 60 feet. We defined a mixed species school as a group of three or more individual fish with at least two species represented. On 3-5 March, we took data on 4 transects, one each at 0, 90, 180, and 270 degrees, swimming for 5 minutes in one direction and recorded numbers of fish in all of the mixed species schools encountered. This was done three mornings between 8:30 and 11:30am and three afternoons between 1:30 and 4:30 pm.

On the same days, after the transect census data was collected, we used the remaining bottom time for each dive to record species compositions for all mixed species schools observed. Most of this observation occurred at a depth of 40 feet and usually lasted about 15 to 20 minutes. Fish were designated as adult, juvenile, or supermale and fish species with no discernible juvenile or supermale stage (e.g., the ocean surgeon) were classified as mature fish.

On 6-8 March, we returned to LTS to a depth of approximately 40 feet and followed the first mixed species school we encountered in the direction of 180 degrees for approximately 36 minutes. Composition of the school was recorded every two minutes and a rock or bolt marked with flagging tape was dropped onto the substrate every four minutes. These were used to estimate distance traveled and direction of travel for each four minute interval. The area covered was estimated by the smallest rectangle enclosing the movements of the school during the 36-minute observation period.

RESULTS

From our transect censuses, we found that there was no statistical difference between the number of schools per transect in the morning and the afternoon ($t = -0.072$, $df = 11$, $P = 0.944$; Table 1) and that there were significantly more individual fish per school in the afternoon ($t = -5.120$, $df = 84$, $P < 0.001$; Table 1).

From our species and age composition data for individual schools, we found no statistically significant difference between species per school in the morning and in the afternoon ($t = 1.776$, $df = 38$, $P = 0.084$; Table 1). There were significantly more juveniles in the morning and significantly more adults, terminal phase males (supermales), and mature fish in the afternoon ($G = 85.105$, $df = 3$, $P < 0.001$; Figs. 1 and 2).

For the four schools we followed, there was a trend of the afternoon schools traveling a shorter total distance ($t = 11.286$, $df = 1$, $P = 0.056$; Table 1) and ranging over a smaller area of the reef ($t = 4.316$, $df = 1$, $P = 0.145$; Table 1).

For frequency data from the four schools surveyed, see Appendix 2.

We found that the composition of a given school changes over time (Figs. 3, 5, 7, and 9). We mapped the route followed by the four schools we observed (Figs. 4, 6, 8, and 10).

TABLE 1. Morning and afternoon differences in mean number of schools per transect, mean numbers of fish per school, mean numbers of species per school, mean distance traveled per 36 minutes, and mean area covered per 36 minutes. Mean ± standard error is indicated.

	Morning	Afternoon
Sch./Tran.	7.08 ± 1.13	7.17 ± 0.92
Fish/Sch.	9.34 ± 0.50	13.83 ± 0.72
Sp./Sch.	4.06 ± 0.18	3.85 ± 0.21
Distance	83.5 ± 12.5 m	63.7 ± 10.75 m
Area	251.25 ± 78.75 m^2	102.88 ± 44.38 m^2

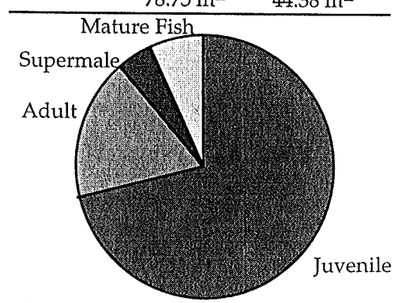

FIG. 1. Age structure of morning schools by frequency.

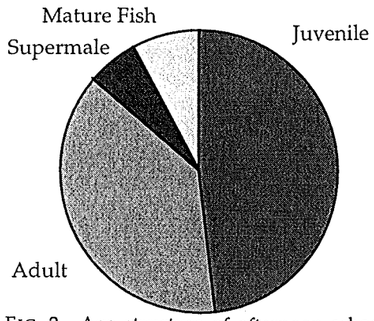

FIG. 2. Age structure of afternoon schools by frequency.

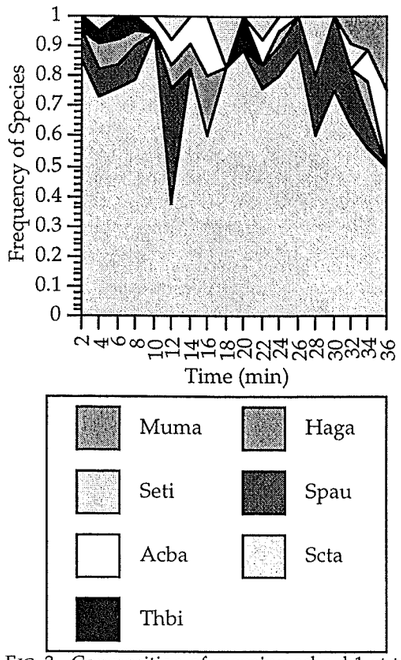

FIG. 3. Composition of morning school 1 at two minute intervals. Legend refers to first two letters of genus and species, see Appendix 1.

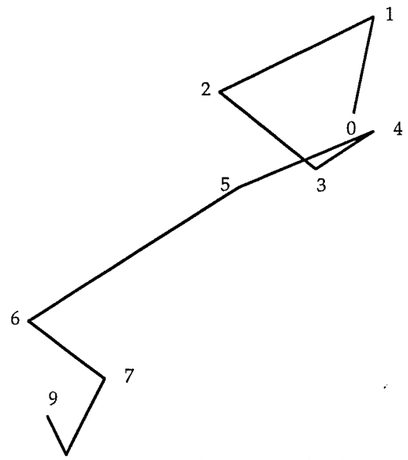

FIG. 4 Movements of morning school 1 over 36 minutes, measured at four minute intervals. 0.19 cm = 1 m, the top of the page is North, 96 total meters traveled, 330 m^2 covered.

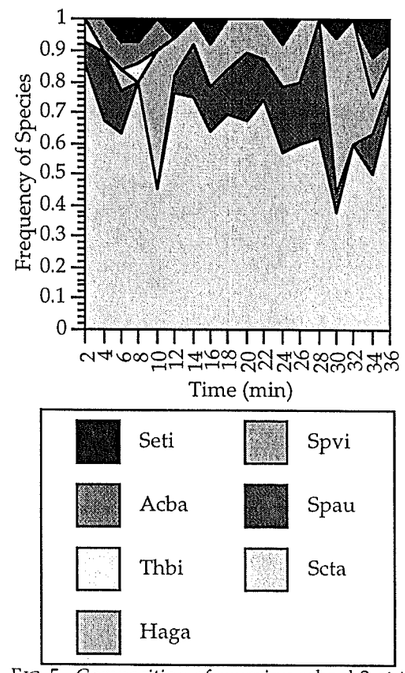

FIG. 5. Composition of morning school 2 at two minute intervals. Legend refers to first two letters of genus and species, see Appendix 1.

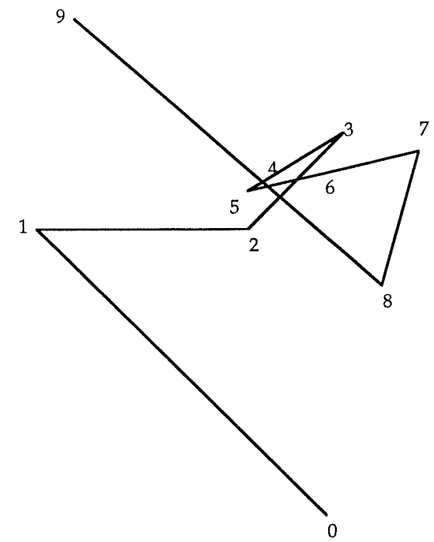

FIG. 6. Movements of morning school 2 over 36 minutes, measured at four minute intervals. 0.38 cm = 1 m, the top of the page is North, 71 total meters traveled, 172.5 m^2 covered.

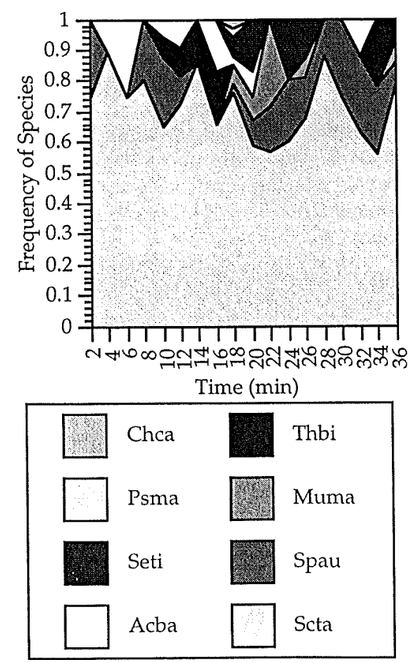

FIG. 7. Composition of afternoon school 1 at two minute intervals. Legend refers to first two letters of genus and species, see Appendix 1.

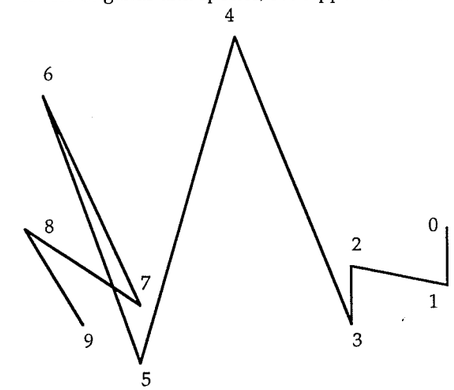

FIG. 8. Movements of afternoon school 1 over 36 minutes, measured at four minute intervals. 0.38 cm = 1 m, the top of the page is North, 74.5 total meters traveled, 147.25 m^2 covered.

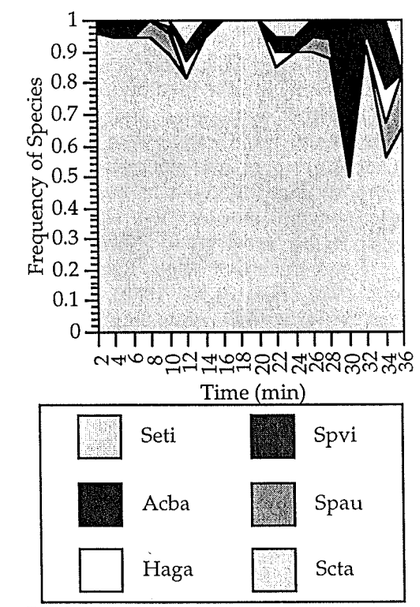

FIG. 9. Composition of afternoon school 2 at two minute intervals. Legend refers to first two letters of genus and species, see Appendix 1.

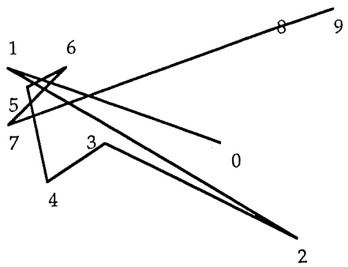

FIG. 10. Movements of afternoon school 2 over 36 minutes, measured at four minute intervals. 0.5 cm = 1 m, the top of the page is North, 53 total meters traveled, 58.5 m^2 covered.

DISCUSSION

As we found no difference in the number of schools obsserved in the morning versus the afternoon in our transect censuses of mixed species schools, it is possible our sampling times may have been too late in the morning to observe schools coalescing. It may be that by 7:00am, most schools have already formed and we may have missed an initial searching phase that occurs in the early morning when fish seek out schools and begin to forage. We did, however, observe more fish per school in the afternoon, supporting our second hypothesis. Several studies have shown increased feeding rates by fish in the afternoon (Bruggeman et al. 1994, Reinthal and Lewis 1986, Hay et al. 1988), and Bruggeman (1994) attributes this pattern to an increase in the potentially digestible organic fraction of algal turfs throughout the day. If food quality is increased in the afternoon, more fish might then be induced to join schools to forage. Both Reinthal and Lewis (1986) and Foster (1985) showed that for two species of tropical herbivorous fish, foraging rates were significantly higher for individuals within a school than for those that were solitary. Schooling may allow fish to swamp territories of other fish where, presumably, algal quality is higher than in undefended areas.

We found more adults than expected in schools in the afternoon and a greater number of juveniles than expected in the morning. Fields et al. (1993) suggested that adults join schools for the purpose of foraging while the primary motivation for juveniles in joining schools was predator avoidance. If this is so, we would expect to see a greater number of adults in schools in the afternoon in proportion to the number of juveniles because of increased food quality in the afternoon. We found no significant difference in the species diversity in the morning versus afternoon. Though there are more individuals in the afternoon schools, the same species may be using the schools in the morning and afternoon.

In our 36 minute continuous observations of schools, fish in afternoon schools tended to travel shorter distances and cover less area than those in the morning. Though these trends are not significant, fish may not have to travel as far or cover as great an area to find better food resources in the afternoon. This may also be a function of the number of fish in the schools in the afternoon. Partridge (1982) stated that as soon as there are three fish in a school, there is no longer a leader. It seems likely that it would be harder to initiate movements in a large school than it would be in a small one. Large schools may employ a strategy of concentrating in one area or patch for a time and then making a large mass movement to another patch, whereas small schools may make more frequent, shorter trips to patches of food.

We noted several patterns of behavior which may be interesting in future study of mixed species schools. For example, some species (e.g., the blue chromis, *Chromis cyanea* and the barred hamlet, *Hypoplectrus puella*) tended to associate with the schools when schools were nearby but were never observed feeding. The harlequin bass, *Serranus tigrinus*, on the other hand, was observed to feed with the school but only when the school was within its territory. In all schools observed we noted only one species of acanthurid in any one school; there was either a blue tang, *Acanthurus coeruleus*, ocean surgeon, *A. bahainus*, or doctorfish, *A. chirurgas*, but never more than one of these three species in a school. We also observed both interspecific and intraspecific aggression within schools. Many questions remain, therefore, as to how fish use mixed species schools and how interactions within the

school may influence the number and types of fish found in them.

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APPENDIX 1: Fish species observed in mixed species schools.

Species	Common Name	Key Name
Acanthurus bahianus	Ocean surgeon	Acba
Acanthurus chirurgas	Doctorfish	Acch
Acanthurus coeruleus	Blue tang	Acco
Chaetodon capistratus	Foureye butterfly fish	Chca
Halichores gamoti	Yellowhead wrasse	Haga
Halichores maculipinna	Clown wrasse	Hama
Holocanthus tricolor	Rock beauty	Hotr
Mulloidichthys martinicus	Yellow goatfish	Muma
Pseudupeneus maculatus	Threespot goatfish	Psma
Scarus iserti	Striped parrotfish	Scis
Scarus taeniopterus	Princess parrotfish	Scta
Serranus tigrinus	Harlequin bass	Seti
Sparisoma atomarium	Greenblotch parrotfish	Spat
Sparisome aurofrenatum	Redband parrotfish	Spau
Sparisoma viride	Stoplight parrotfish	Spvi
Thalassoma bifasciatum	Bluehead wrasse	Thbi

APPENDIX 2: Observed frequency composition at two minute intervals of individual fish species from four 36 minute surveys . Fish species are referred to by the first two letters of genus and species, see Appendix 1.

Morning School 1

	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36
Acba	0	0	0	0	0	.06	.08	.09	.20	0	0	.08	.05	0	0	0	0	.11
Haga	.05	.09	.08	.05	.05	0	.08	.09	.20	0	0	0	.05	0	0	0	0	.11
Muma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	.09	.11
Scta	.85	.72	.76	.79	.79	.94	.38	.82	.60	.83	.89	.76	.80	.89	.60	.75	.64	.56
Seti	0	.05	0	0	0	0	.08	0	0	.17	0	.08	0	0	.20	0	.09	0
Spau	.10	.09	.08	.11	.11	0	.38	0	0	0	0	.08	.10	.11	.20	.25	.18	.11
Thbi	0	.08	.08	.05	.05	0	0	0	0	0	.11	0	0	0	0	0	0	0

Morning School 2

	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36
Acba	0	.11	.09	.07	.10	0	0	0	0	0	0	0	0	0	0	0	.13	.06
Haga	0	0	.07	0	.45	.12	.08	.14	.16	.11	.13	.14	.20	0	.50	.40	.12	.07
Scta	.86	.67	.63	.80	.45	.76	.75	.64	.69	.67	.74	.57	.60	.62	.38	.60	.50	.73
Seti	0	0	.07	.07	0	.06	0	.08	0	0	0	.08	0	0	.06	0	.12	.07
Spau	.07	.22	.14	0	0	.06	.17	.14	.15	.22	.13	.21	.20	.38	.06	0	.13	.07
Spvi	.07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thbi	0	0	0	.06	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Afternoon School 1

	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36
Acba	0	.11	.25	0	.06	.09	0	.17	.03	.08	0	0	0	0	0	.12	0	0
Chca	0	0	0	0	0	0	0	0	.03	0	0	0	0	0	0	0	0	0
Muma	0	0	0	0	0	0	0	0	.06	.08	.29	0	.06	0	0	0	0	.07
Psma	0	0	0	0	0	0	0	0	.03	0	0	0	0	0	0	0	0	0
Scta	.75	.89	.75	.80	.65	.73	.86	.66	.76	.59	.57	.60	.68	.88	.75	.63	.56	.79
Seti	0	0	0	0	0	0	0	0	.06	.17	0	.20	.13	0	0	0	0	0
Spau	.25	0	0	.20	.23	.09	0	0	.03	.08	.14	.20	.13	.12	.25	.25	.22	.07
Thbi	0	0	0	0	.06	.09	.14	.17	0	0	0	0	0	0	0	0	.22	.07

Afternoon School 2

	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36
Acba	.04	.05	.05	.05	0	.05	.05	0	0	0	.05	.05	.05	.06	.50	.04	.22	0
Muma	0	0	0	0	.02	.05	0	0	0	0	.05	0	0	0	0	.04	.11	0
Scta	.96	.95	.95	.95	.89	.82	.95	1	1	1	.85	.90	.90	.88	.50	.92	.56	.66
Seti	0	0	0	0	0	.08	0	0	0	0	.05	.05	0	0	0	0	0	.17
Spau	0	0	0	0	.07	0	0	0	0	0	0	0	.05	.06	0	0	.11	.17
Thbi	0	0	0	0	.02	0	0	0	0	0	0	0	0	0	0	0	0	0